POSITIVE FEEDBACK MECHANISMS AND PLANT DISEASE

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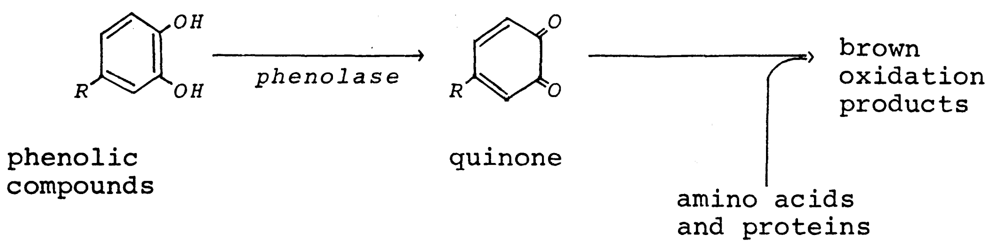
ABSTRACT

A novel biochemical concept of a positive feedback system is suggested based on the reactions occurring in apple fruit infected with *Penicillium expansum* or plants suffering from boron deficiency.

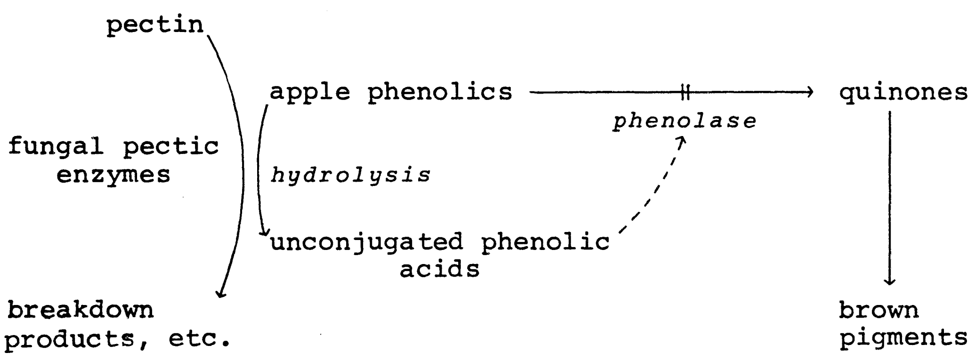
Many biosynthetic processes in plants and animals are controlled by some sort of feedback process. This control mechanism may be a simple end-product inhibition of an enzyme where the product of the reaction $A \rightarrow B$ inhibits the enzyme concerned and thus regulates the process. In more complicated pathways of biosynthesis such as $A \rightarrow B \rightarrow C \rightarrow D$ the end-product D may inhibit or regulate the first enzyme of the sequence and this is called allosteric inhibition. In both cases the net result is for the level of end-product to control the initial rate of reaction and thus the final level of end-product; in other words the system is self-regulating.

Very similar self-regulating processes are used in electronic systems (such as hi-fi amplifiers). For example, if the end-product or signal is arranged to control or decrease the process or degree of amplification the system is said to operate "negative feedback control". By contrast, in a situation where the feedback signal *increases* the gain of the amplifier, so as to make it oscillate, the system is said to show "positive" or "regenerative" feedback. Such positive feedback processes are quite common in electronic systems, but are rare in biological systems. It is the purpose of this article to illustrate two biochemical processes involved in plant disease, which may be considered to establish a form of positive feedback.

The first positive feedback system to be considered is concerned with biochemical processes that take place when an apple is infected with the fungus *Penicillium expansum* or "blue-mould". No doubt most people are familiar with the browning that occurs when the flesh of an apple, or potato or other fruit is damaged. An enzyme in the fruit called diphenol oxidase (*DPO*) causes this browning by acting upon a number of phenolic compounds or "tannins" already present in the fruit cells. This browning reaction is considered to play a major role in the plant's defence mechanism since the initial reaction of the phenolase system is to yield highly reactive quinone-compounds which may combine together to form a complex brown polymeric material which seals off the damaged cell: this may be considered in some ways analogous to the blood clotting process in the animal. Moreover, these reactive quinones will also combine with amino acids and proteins, thus inactivating the proteins (enzymes, etc.) of an invading pathogen. These reactions are summarised below:



In the special case of an apple infected with *P. expansum* this enzymic browning defence mechanism is rendered in-operative as can be seen by the fact that the rotted fruit tissue does not turn dark brown as is the usual case. Results of an investigation of this problem by the author suggested that the following pattern of events was taking place:



P. expansum secretes powerful pectolytic enzymes which break down the pectin "cement" which holds the plant cells together, hence the infected tissue becomes semi-liquid in consistency and the fruit disintegrates. These fungal pectolytic enzymes are also able to hydrolyse some of the apple's phenolic compounds to yield simpler phenolic acids which have been shown to be powerful inhibitors of apple phenolase.

p-coumaryl-quinic acid ⟶ *p*-coumaric acid
↓
chlorogenic acid ⟶ caffeic acid
hydrolysis
↓ *methylation* ↓
feruloyl-quinic acid - - - - - - - → ferulic acid

Thus we have a situation in which the fungus uses the substrates for the apple's defence mechanism to provide a source of material for the inhibition of this mechanism and by analogy with the electrical system this may be considered to be a positive feedback process.

I am aware of only one other system which would be considered to show a positive feedback reaction and that is concerned with the effects of boron deficiency in plants. In 1967 Lee and Aronoff presented evidence that suggested that boron, as the borate ion, controlled the partitioning of glucose metabolism between glycolysis and the pentose shunt pathway. This controlling effect was brought about because borate appeared to form a complex with 6-phospho-gluconate which subsequently inhibited 6-phospho-gluconate dehydrogenase. The activity of the pentose phosphate shunt pathway controls the supply of intermediates such as erythrose-4-phosphate, which combines with phospho-enol pyruvate, from the glycolytic pathway, to yield shikimic acid, phenylalanine, and eventually phenolic acids (Fig. 1).

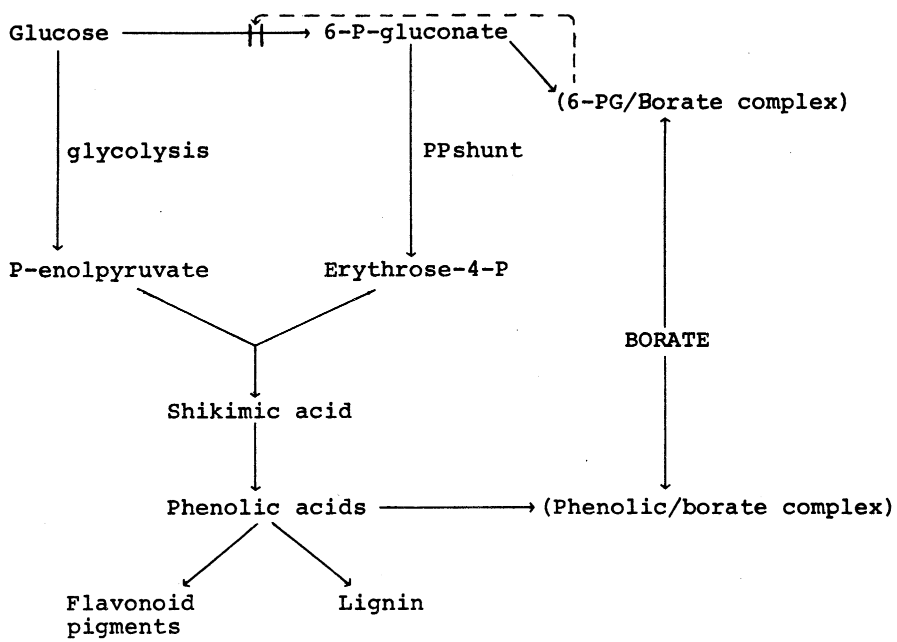


Fig. 1. Diagram to show the biochemical effects of boron deficiency (based on data of Lee and Aronoff, 1967).

Certain dihydroxy-phenolic acids also form strong complexes with borate causing a diminution of the amount of borate available to complex with 6-phosphogluconate. This results in a release of the inhibition of the 6-PG dehydrogenase and the subsequent formation of an excess of phenolic compounds to complex the remaining borate. Thus an autocatalytic or positive feedback system is set up which generates an excess of phenolic acids leading to tissue necrosis and the eventual death of the plant.

I would be interested to learn of other similar systems which could be considered to operate "positive feedback" processes.

ACKNOWLEDGMENT

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